# A NEW *TROCHILISCUS* (CHAROPHYTA) FROM THE DOWNTONIAN OF PODOLIA EASTERN EUROPE

BY

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# A NEW *TROCHILISCUS* (CHAROPHYTA) FROM THE DOWNTONIAN OF PODOLIA

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## SYNOPSIS

*Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. is described from beds of Lower Devonian (Downtonian) age from the Podolian of eastern Europe. It is the earliest species of the genus and the earliest Charophyte of which there is reliable evidence. The fruits are unusually well preserved and permit detailed comparison to be made with the lime-shell, oospore membrane, and oospore contents of Recent and fossil Charophytes. The fresh evidence amply confirms the Charophyte affinity of the genus. The classification of *Trochiliscus* is discussed and the species are grouped into two new sub-genera, *Eutrochiliscus* and *Karpinskya*. It is concluded from a review of the geological occurrences of *Trochiliscus* and *Sycidium*, and from the nature of their oospores, that they were probably land-plants, growing, like the Recent Charophyta, in fresh or brackish water.

The structure of the Oligo-Miocene species *Chara escheri* is found to agree in detail with that of living *Chara*.

## I. INTRODUCTION

THE fossils placed in the genus *Trochiliscus* differ from post-Lower Carboniferous and Recent charophyte fruits in that the spiral enveloping cells number more than five, and have a right-hand, not a left-hand, twist. They were first discovered nearly 100 years ago in the Devonian of north-west Russia, and were later recognized in the same formation in North America. During the latter half of last century they were assigned to groups in both the plant and animal kingdoms, especially the Foraminifera. Quenstedt (1867:843) was one of the first to compare these bodies with charophyte fruits. A few years later the first American examples were described by Meek (1873) as probably the fruits of *Chara*. But it was not until the appearance of Karpinsky's admirable and elaborate monograph in 1906, which was based on the European trochilisks[1]—*Trochiliscus* and *Sycidium*—that sound reasons were given for placing these genera in the Charophyta. This view was not, however, generally accepted, and it was left to Peck in 1934, as a result of a detailed study of the North American species of *Trochiliscus*, a study which proved as fruitful as Karpinsky (1907) had predicted, to provide convincing evidence that this genus was correctly placed in the Charophyta. That evidence—particularly the discovery of species with calcified coronula cells—is now supplemented by a fuller knowledge of the structure of

[1] Pander (1856: 17; 1857: 13) and all later writers in German use the vernacular term *Trochilisken*. Karpinsky (1907: 123) also uses the French *trochilisques*. Hecker (1941) writes *trochilisks*, and this is presumably the correct form in English.

the fruit given by the unusually well-preserved remains of a new species from eastern Europe.

The interest of the trochilisks lies partly in the fact that they are the most typical calcareous Algae of the Devonian period, and partly in the evidence they give of the very early adaptation of marine Algae to fresh- or brackish-water conditions.

Grateful acknowledgements are made to all those who have assisted in the preparation of this paper: to Mr. G. O. Allen for valuable discussions on problems relating to living charophytes and for the loan of Recent material; to Prof. W. H. Lang for criticism and advice; to Prof. T. M. Harris for helpful discussions; to Mr. W. N. Edwards for advice and encouragement; to Mr. F. M. Wonnacott for help, especially with the bibliography; and to Mr. J. E. Owen for much practical assistance.

Prof. R. E. Peck has very kindly read through the paper and made some valuable suggestions.

## II. LOCALITIES AND HORIZONS OF *TROCHILISCUS*

The specimens of *Trochiliscus* and *Sycidium* in the Pander and Volborth collections described by Karpinsky (1906: 107) came mainly from the neighbourhood of Pavlovsk, which is 30 km. south-south-east of Leningrad. Localities in Esthonia, Dorpat (now Tartu) and Isborsk (now Irboska), were also mentioned. In the Baltic States, and in the Leningrad and Kalinin areas of Russia, not only is the whole of the Lower Devonian missing, but also the basal part of the Middle Devonian. Recent Russian work, summarized by Hecker (1941: 75 et seq.), shows that the Leningrad localities occur in the two lowest of the four stratigraphical divisions of the Middle Devonian of the Main Devonian Field, in beds resting unconformably on planed Cambrian and Ordovician rocks. These divisions, the Pärnu and Narova beds, which are assigned to the Upper Middle Devonian (Givetian) by Jarvik (1949: 42), contain abundant trochilisks, whereas none appear to be present in the two overlying divisions. Trochilisks are also stated to occur in local abundance in certain divisions of the Upper Devonian, but *Trochiliscus* is not mentioned by name and the reference is probably to *Sycidium*. In Esthonia trochilisks, presumably both *Trochiliscus* and *Sycidium*, occur in the same Middle Devonian beds as in the Leningrad area, and have given their name to the 'Trochilisken-Sandstein' (Orviku, 1930). This recent work amplifies Karpinsky's general statement that the Russian trochilisks were obtained from beds belonging to the Middle, and the lower part of the Upper, Devonian (Karpinsky, 1906: 114).

The North American material described by Peck (1934, 1936) came from several localities and horizons of Devonian and basal Mississippian age. The youngest horizon, the Sylamore sandstone of central Missouri, is now known as the Bushberg sandstone (Branson, 1944: 176, 185). The oldest specimens, with the possible exception of those from the shale below the Mineola limestone, are from the Jeffersonville and Columbus limestones of Onondaga age, which are placed by Cooper *et al.* (1942) in the uppermost Lower Devonian (Coblentzian) of the European succession.

More recently, *Trochiliscus* has been obtained in cores from 'near the base of the Onondaga formation' in south-west Ontario, Canada (Fritz, 1939). Dr. Fritz has kindly informed me (*in litt.*, September 1950) that this material has not been described.

Lastly, some minute, more or less spherical, calcareous bodies have been described from the Devonian of Texas, U.S.A., as 'questionable internal molds of trochiliscid oogonia' (Ellison & Wynn, 1950: 795, pl. 1, figs. 1–7). The horizon is uncertain, but a Lower Devonian age is possible. The bodies are associated with conodonts and fish-remains in a basal glauconitic sandstone resting on strata assigned to the Silurian.

The Russian, Esthonian, and North American localities have provided all the known material of *Trochiliscus*. The species described below is from a new area, west Podolia, on the borders of Poland and Russia. The specimens were found by Mr. H. A. Toombs in the rock matrix of the W. Zych collection of fishes which was acquired by the British Museum (Natural History) in 1935. They came from fish-beds in the Czortkov series of the Downtonian of Podolia and are labelled 'Polen. Podolien. Jagielnica [or Jagielnica Stara]. Old Red.' The town of Jagielnica (lat. 48° 57′ N.; long. 25° 45′ E.) is 150 km. south-east of Lvov and 16 km. south-west of Czortkov. Jagielnica Stara is 5 km. south-south-east of Jagielnica. Dr. Zb. Sujkowski-Leliwa informs me that in this area the Czortkov series has a very gentle dip to the west, is unfaulted, and that the beds at these two places are therefore at approximately the same horizon. This is supported by the lack of any obvious lithological difference in the matrices and by the identity of the *Trochiliscus* remains from the two localities. The majority of the specimens described below are from the Jagielnica locality.

The age of the fish-beds is accurately determined as early Lower Devonian (Downtonian = lower Gedinnian). Stensiö (1944: 4, footnote) records *Corvaspis* in the fish fauna from Jagielnica Stara and correlates these uppermost beds of the Czortkov series with the late Downtonian strata in England and Spitsbergen in which this genus occurs. According to the zonal classification of White (1950: fig. 1), *Corvaspis* is restricted to the highest beds of the Downtonian (Lower Old Red Sandstone) in the Anglo-Welsh area. (See also Westoll (1951) for detailed correlations of the European Devonian.) It is certain therefore that the Podolian *Trochiliscus* is older than the previously described species from Russia and North America; and, unless the Silurian age of '*Pseudosycidium*' from Turkestan (Hacquaert, 1932) should be confirmed, it is the earliest charophyte of which we have reliable evidence.

## III. MATERIAL AND METHODS

The pale buff-coloured matrix containing the fossil fruits consists of siltstone with harder layers of fine calcareous sandstone. The fruits, all of which belong to one species, are conspicuous on weathered and broken surfaces as shown by specimens V.27158–V.27171.[1] Their preservation is unusually good. The outer shell consists of cloudy or banded calcite without silicification, and remains of the organic contents are preserved in the clear crystalline calcite which fills the central cavity. Deposits of pyrite or reddish-brown granular mineral (which are readily distinguishable from carbonaceous material by reflected light) are sometimes present in the central cavity and in the apical or basal openings.

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[1] The registered numbers refer to specimens in the Geol. Dept., British Museum (Natural History).

The abundant material was studied by the following methods. Harder layers, in which the fruits comprise perhaps 20 per cent. of the rock by bulk, were made into thin ground sections which gave useful information as to the morphology of the gyrogonite. Most of the work, however, was done on material isolated from the matrix.

The siltstone breaks down when boiled for several hours in dilute sodium carbonate solution and the fruits can be concentrated by washing, and cleaned with a sharp needle on a glass slide coated with plasticine. Several hundred specimens were extracted from a few cubic centimetres of the rock and, as Pander wrote of the Leningrad material, could no doubt be obtained 'by the bushel'. Many of them show some degree of distortion attributable to compaction of the sediment. The external measurements of the gyrogonites given below were obtained from about 100 specimens all of which showed spiral ribbing. A few of the gyrogonites which have no spiral ornament and do not at first sight seem to belong to the normal form owe their different appearance to corrosion. Vertically ribbed or pitted bodies which could be attributed to *Sycidium* are absent.

No vegetative axes of the parent plant, such as those which were associated with the Russian trochilisks (cf. Karpinsky, 1906: figs. 46–57), have been found with the fruits.

Examination and photography of these minute bodies were greatly assisted by whitening them with a thin deposit of ammonium chloride by means of the simple but effective apparatus described by Teichert (1948). The deposit being much heavier on the ridges than in the furrows, the ridges become more strongly emphasized.

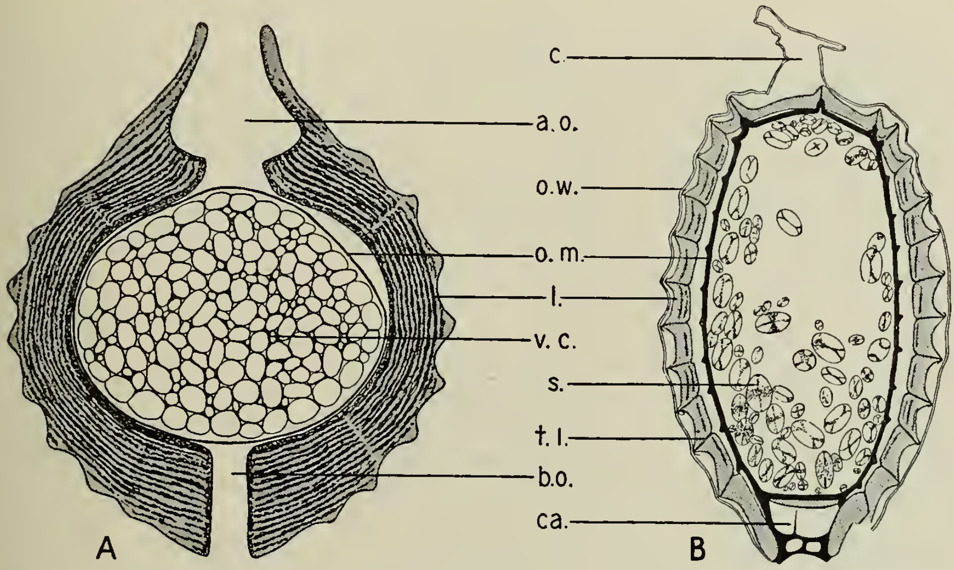
In order to obtain mounts of the delicate organic contents of the fossil gyrogonites, the bodies were gently dissolved in 1 per cent. HCl and the insoluble remains were transferred direct to gum chloral by pipette, without further treatment, and covered.

Ground sections of the isolated gyrogonites were made by first embedding them, either singly or in groups, in the transparent plastic, 'Marco' resin (Purves & Martin, 1950). Sections of the gyrogonites of Recent and fossil Charas were made in the same way.

## IV. DESCRIPTION OF THE MATERIAL

The terminology of the following description is mainly that adopted by Peck (1934: 104). Harris (1939: 12) in reviving the term *gyrogonite* pointed out that 'it is not quite accurate to term the calcareous body found fossil the "oogonium", as most authors do, since it is but the calcareous inner part of the oogonium' (using the latter term to mean the egg-cell together with its sheath of sterile enveloping cells). The term *gyrogonite,* which may well be used to include all fossil charophyte fruits irrespective of the number and direction of the enveloping cells, is accordingly used here in preference to *oogonium.* The phrase 'gyrogonite non-coronulate' may then be employed without prejudice to the view that the female organ probably had a coronula which left no trace on the gyrogonite, either because it was minute or deciduous, or because it was never calcified. The term *oogonium* is in any case liable to be misunderstood for, as used by German authors, it generally applies to the egg-cell alone, which is the only part of the female organ that is homologous with the oogonium in other Algae (see Moll, 1934: 117; Smith, 1938: 130; Wood, 1947: 241; Fritsch, 1935). *Egg-bud*, the English equivalent of Sachs's term *Eiknospe* (see Oltmanns, 1922: 449)—an unexceptionable name for the female organ—has only recently been introduced (Maslov, 1947).

The term 'lime-shell' (Groves & Bullock-Webster, 1920: 74) is used for the calcareous wall of the fruit. It encloses the thickened oospore membrane (*Hartschale*) which in turn encloses the mature ovum. The terms *cellular* and *intercellular*, as applied to the sculpturing of the lime-shell, have been defined by Peck (1934: 104). The use of these and other terms is illustrated in Text-fig. 1.



Text-fig. 1. A. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. L. Devonian. Restoration of gyrogonite in median longitudinal section. ×120. B. *Chara hispida* L. Fruit of Recent species in median longitudinal section in polarized light. ×70. (V.28356.) Cf. Groves & Bullock-Webster (1924: pl. 31, fig. 6).

*a.o.*, apical opening; *b.o.*, basal opening; *c.*, shrivelled remains of coronula; *ca.*, cage, enclosing the winding cell, node-cell, and (?) stalk-cell; *l.*, lime-shell; *o.m.*, oospore membrane; *o.w.*, outer wall of fruit; *s.*, starch-grains, many of which have fallen away; *t.l.*, thickened lateral walls of spiral cells; *v.c.*, vesicular contents. The furrows on the lime-shell of *Chara*, and probably of *Trochiliscus*, are *cellular*, and the ridges *intercellular*.

## *CHAROPHYTA*

### Family TROCHILISCACEAE

### Genus ***TROCHILISCUS*** Karpinsky 1906

Grounds for rejecting the name *Calcisphaera* and for attributing the authorship of the genus to Karpinsky are given by Peck (1934: 105). The status of the problematical Carboniferous genus *Calcisphaera* Williamson has been discussed by Pia (1937: 803). In spite of imperfect figuring and description it is almost certain that *Moellerina greenei* Ulrich is a *Trochiliscus*, probably conspecific with *T. devonicus* from the same locality (see below, p. 206). Should this be confirmed on the discovery of the type material, a case could be made for conserving the comparatively well-known name *Trochiliscus*

### Sub-genus EUTROCHILISCUS nov. (see p. 209 below)

### ***Trochiliscus* (*Eutrochiliscus*) *podolicus*** n.sp.

(PL. 18; PL. 19, FIGS. 17–19; TEXT-FIGS. 1–4)

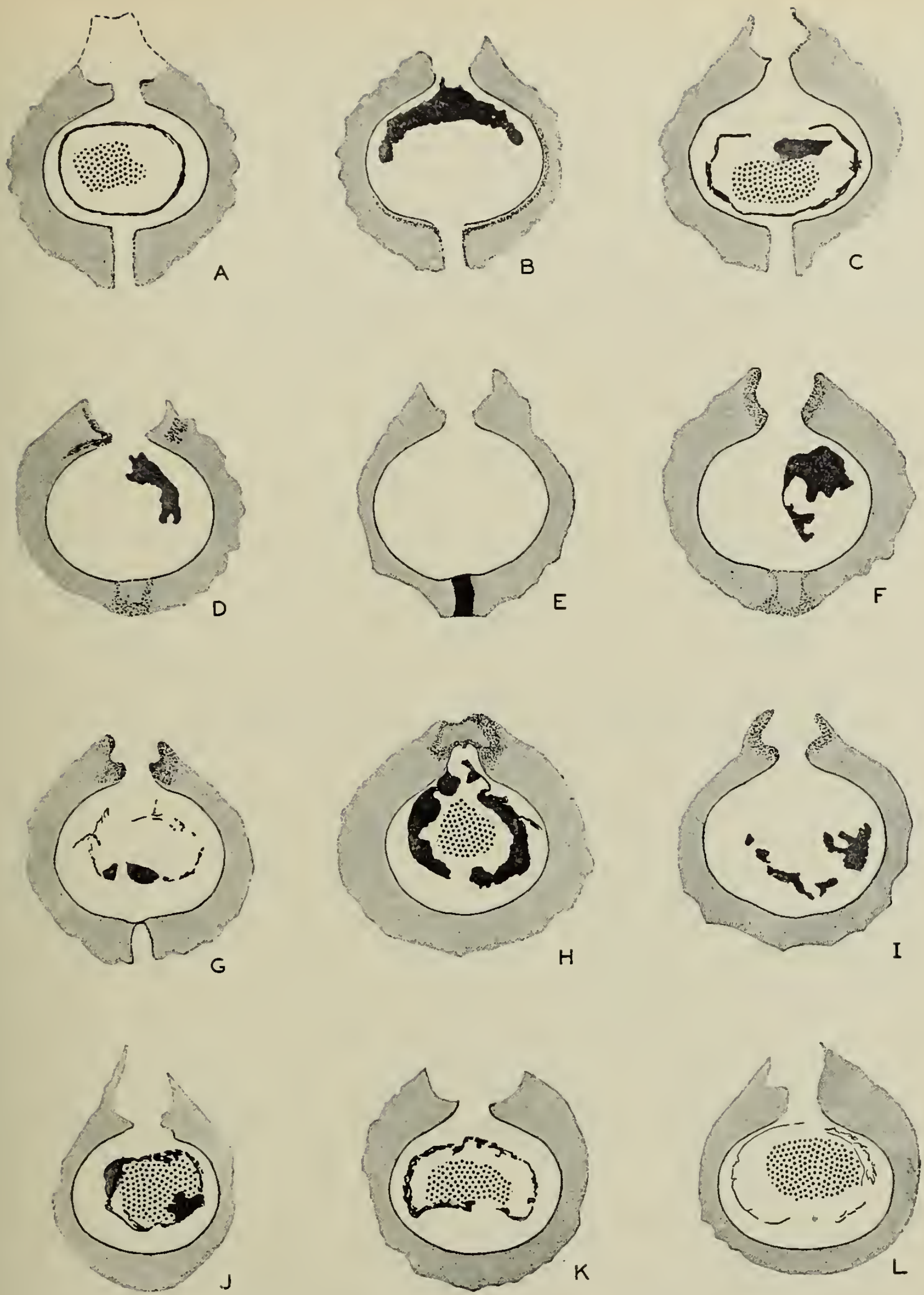
DIAGNOSIS. Gyrogonite non-coronulate, bulbiform; diameter 530 $\mu \pm 20$ per cent.; length including apical beak 580 $\mu \pm 20$ per cent. Ridges 10, making rather more than a complete turn round gyrogonite, moderately sharp with rounded furrows between; equatorial angle approximately 20°; about 10 to 12 ridges seen in lateral view. Apical opening expanded in middle part, proximally about 60 $\mu$ wide. Basal opening cylindrical, about 40 $\mu$ in diameter. Lime-shell concentrically laminated with *c.* 3–5 $\mu$ spacing between bands. Oospore membrane very thin (1 $\mu$), generally brown and translucent with fine granulate decoration.

HOLOTYPE. V.28340. Geol. Dept., B.M. (N.H.).

LOCALITIES AND HORIZON. Jagielnica and Jagielnica Stara, west Podolia. Fish-beds in Czortkov series; Lower Devonian (Downtonian).

DESCRIPTION: *General Morphology*. The somewhat variable shape and size of the gyrogonite in lateral view is indicated in Pl. 18, figs. 1–5, and Text-fig. 2. Pl. 18, figs. 4 and 5 are examples of specimens with a pronounced apical beak. In the majority of specimens, however, the beak is poorly developed, either because it was originally incompletely calcified, or because it was subsequently broken off. The base of the gyrogonite is rounded, or slightly produced (Pl. 18, figs. 6, 7). Out of 100 specimens measured, 97 were found to have a breadth of 530 $\mu \pm 20$ per cent., and 90 an overall length of 580 $\mu \pm 20$ per cent., the remainder lying just outside these ranges. The size variations are shown in the frequency diagrams in Text-fig. 4.

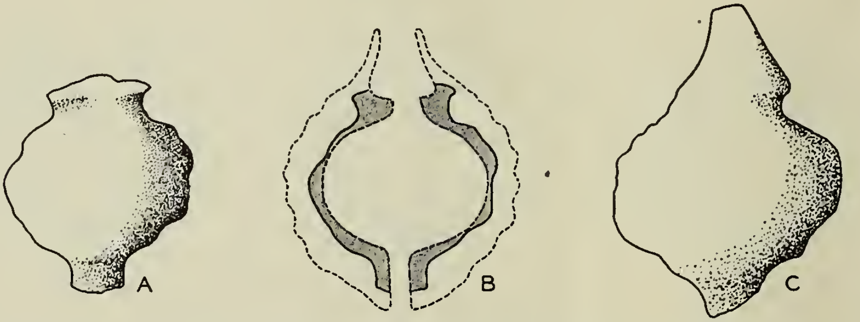
The dextrally spiralled ridges are moderately sharp with rounded furrows between. The prominence of the ridges may vary on different areas of the same specimen, due to incomplete removal of the matrix or to abrasion. In Pl. 18, figs. 1–5 the ridges appear blunted due to the somewhat granular coating of ammonium chloride. In thin sections of the rock the outline of the lime-shell is often indefinite (Pl. 18, fig. 8) and the ridges and furrows are usually less well shown than by some of the sections of isolated specimens (Pl. 18, fig. 7). The equatorial angle of the ridges varies from about 17° to 24°. The ridges make approximately $1\frac{1}{4}$ turns round the gyrogonite, and, on passing on to the beak, become sub-parallel to its axis (Pl. 18, figs. 4, 5). It is usually possible to count 10 to 12 ridges in lateral view. In only 11 specimens was the base well enough preserved to allow the number of ridges to be counted with certainty. These all showed 10 ridges springing from a small basal opening. They are clearly seen in the holotype, Pl. 18, fig. 2.



TEXT-FIG. 2. A–L. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Somewhat diagrammatic drawings of gyrogonites in approximately median longitudinal section. All ×60. Light tone = lime-shell; dark tone = oospore membrane; stippling = remains of oospore contents. (A–E, V.28348; F, V.28351; G–K, V.28349; L, V.28350.)

The apical and basal openings are often marked by a zone of brown staining in the surrounding lime-shell, as indicated by shading in Text-fig. 2. This staining, which contrasts with the light-coloured matrix filling the openings, may be seen in sections, and in surface view when the gyrogonite is immersed in xylol. In median longitudinal sections (Pl. 18, figs. 6, 7) the basal opening is more or less cylindrical with a maximum length of about 140 μ; in surface view under xylol it is circular in section with a diameter of about 40 μ (20 μ–60 μ).

The apical opening differs in shape and size from the basal opening. This is well seen in Pl. 18, figs. 6 and 7, especially the first, which shows both openings filled with dark material. Traced outwards the apical opening at first decreases more or less rapidly to a diameter of approximately 60 μ, and then expands rather suddenly to nearly three times this width: thereafter the diameter slowly decreases until the apex of the beak is reached (Text-fig. 2J). The lime-shell becomes thin where the opening reaches its greatest diameter, and the apex is often broken off along this line of weakness. This description is supported by the examination of specimens in surface view, for the ends of the more prominent beaks are only about 100 μ across, or somewhat less, and in these the opening at the tip does not exceed a diameter of 75 μ. The opening is, however, considerably larger when the beak is missing. The rather variable appearances of the apical opening as shown in Text-fig. 2 may be explained by the degree of obliquity[1] of the sections; by more or less incomplete preservation of the beak; or by individual variations. The clear calcite of the central cavity usually extends into the narrow part of the opening, the expanded portion being filled with matrix.



Text-fig. 3. A–C. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Corroded gyrogonites. In B, the relation between the corroded and the normal forms is indicated diagrammatically. (A, V.28593; C, V.28594. × *c.* 60.)

The corroded gyrogonites (Text-fig. 3) are, on the average, decidedly smaller. The degraded beak is often delimited from the body of the gyrogonite by a shallow groove giving the gyrogonite a rather distinctive appearance. There may also be a small, but prominent, basal projection. A few specimens with these characters have been detected in thin sections of the rock.

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[1] Cf. Pia (1936: 45) on the differing appearances of random sections through short cylinders.

Sections of the gyrogonites show an outer cloudy or dark zone—the lime-shell—which is sometimes closely banded, and an inner mass of clear calcite occupying the central cavity. The organic contents preserved in the calcite comprise a contracted organic membrane, interpreted as the original oospore membrane; and within this a brownish mass, sometimes showing a well-marked vesicular structure, which is regarded as the remains of the ovum. The organic contents appear as a dark patch when the gyrogonite is immersed in xylol. The granular nature of the lime-shell is indicated by the fact that thin sections remain illuminated throughout a complete rotation between crossed nicols. The clear calcite filling the central cavity, on the other hand, consists of a few large crystals which may be partially bounded by the contracted oospore membrane. The lime-shell, oospore membrane, and vesicular contents will be described in turn.

*Lime-shell.* The thickness of the lime-shell at the equator varies from about 40 $\mu$ to 70 $\mu$, but in a few specimens it is much thinner. The inner surface is smooth without ribs or furrows. In sections of the majority of specimens the lime-shell appears to be structureless. In others there is a more or less definite indication of a concentric layering or lamination, which is clearly demonstrated in a few well-preserved specimens. Thus the specimen in Pl. 18, fig. 9, part of which is enlarged in Pl. 18, fig. 10, shows a concentric banding of light and dark laminations. They are still more clearly marked in Pl. 18, fig. 11, which also shows that they may end abruptly in a structureless portion of the lime-shell. The spacing of the dark laminations in different specimens is remarkably constant, ranging from 3 $\mu$ to 5 $\mu$. In the two specimens figured and in others the layers are only slightly rippled. In none of the numerous sections examined is there any undulation at all comparable in amplitude or wave-length with that of the ridges or furrows. In Pl. 18, fig. 12 the indistinct layering appears to be more or less concentric and certainly does not reflect the strong undulations of the ridges and furrows. There are few indications of radial interruptions in the layering, and these are too irregularly spaced to suggest the positions of the lateral walls of spiral enveloping cells.

*Oospore membrane.* A contracted continuous membrane, often broken up by numerous cracks and considerably disrupted, is present in most, if not all, of the gyrogonites. A good example of a membrane in approximately optical section is shown in Pl. 18, fig. 7; others are represented in Text-fig. 2. Under high power the membrane is found to be very thin, and is uniformly about 1 $\mu$ thick. Because of the clearness of the calcite, the membrane appears much thicker in oblique optical section, and is thus represented in some of the drawings in Text-fig. 2. The specimen in Pl. 18, fig. 8 is unusual in that the membrane is double as though an inner and an outer layer had separated. The outer layer is somewhat thicker and darker than the inner; but their combined thickness does not exceed 1 $\mu$. The contraction of the membrane is usually greater away from the basal end of the gyrogonite, and the displaced membrane sometimes projects towards, or even extends into, the expanded portion of the apical opening. The symmetrical structure in Pl. 18, fig. 14, however, is not a mere projection of the oospore membrane but a distinct 'appendage' with a thinner and more translucent wall. A simple explanation of it would be that it is a contracted membrane which lined the lower part of the apical opening and did not become involved in the thickening of the oosphere wall. It has not, however, been observed in any other specimen.

The membrane is readily isolated by decalcification of the gyrogonite and its characters are then studied more easily. Sometimes the more or less globular shape is retained (V.28557). The membrane is usually translucent and pale to dark brown by transmitted light, but it may be black and opaque. The more translucent membranes are decorated with small irregular granules, as in Pl. 19, fig. 17, which is magnified ×500. A similar, but coarser, decoration, seen in Pl. 19, fig. 18 at the same magnification, is exceptional. A few of the membranes examined have scattered (sometimes contiguous), more or less circular, thicker areas, about 3–5 $\mu$ in diameter, some of which have a minute central pore. Examples of these thickenings, which are sometimes partially torn away from the membrane, leaving a rent, are shown in Pl. 19, fig. 19. None of the membranes has any parallel ridges or lines on its surface.

*Vesicular contents of oospore.* In ground sections of many specimens the brown contents lying within the oospore membrane resemble patches and wisps of disorganized tissue. Others show a definite cellular pattern, as in Pl. 18, fig. 14. Pl. 18, fig. 13 is a section showing a distinct, rounded margin to the vesicular body. In this, as in most other specimens, the contents have undergone greater contraction than the enveloping membrane. The best demonstration of the vesicular structure and of the globular form is afforded by decalcified specimens. Pl. 18, fig. 15 shows one of the spherical bodies, 240 $\mu$ in diameter, still enclosed within the partially ruptured oospore membrane. In Pl. 18, fig. 16 a similar specimen, freed from the membrane, is shown at a higher magnification. The rather uniform, frothy tissue is made up of rounded vesicles, which are frequently oval in optical section. The outer walls of the vesicles are convex, and there is no evidence that the vesicular mass had its own investing membrane. In these two examples the major axes of the vesicles measure about 25 $\mu$; in less contracted specimens they may reach 40 $\mu$.

DISCUSSION. This species is distinguished from *T. ingricus* by the much smaller number of spiral ridges; and from *T. bulbiformis*, which it resembles in shape, by its greater size (diameter about 530 $\mu$ compared with 250–400 $\mu$). The number of ridges is also different, being 10 instead of 8 or 9. It differs from the North American species *T. convolutus* (*T. minutus* and *T. multivolvis*) in the much greater convolution of the ridges (360°+ compared with 180°+), and it is also somewhat larger (average diameter 530 $\mu$ compared with 300–400 $\mu$). Disregarding the doubtful forms *T. lemoni* and '*Moellerina greenei*', *T. podolicus* is the most convolute *Trochiliscus* known.

Karpinsky showed that his species *T. ingricus* normally had 18 spiral ridges, corresponding to 18 spiral cells. From analogy with some American specimens which have two ridges in each cell, Peck (1936: 765) concluded that there were probably only 9 spiral cells. If this were so, 18 ridges or furrows on the outside of the lime-shell would correspond to 9 ridges or furrows on the inside of the shell. But Karpinsky's figures of a section through the gyrogonite show 18 ridges and furrows on both the inner and outer surfaces (Karpinsky, 1906: pl. 2, fig. 28; text-fig. 31). Sections made of topotype material kindly loaned by Prof. T. G. Halle from the Riksmuseum Collections confirm Karpinsky's figures. Owing to the steepness of the spirals an equatorial section cuts all the ridges almost at right angles. The meeting of a pair of ridges in a V near the pole is not in itself evidence that both ridges belong to one cell (see, for example, Peck, 1934: pl. 10, figs. 23, 24).

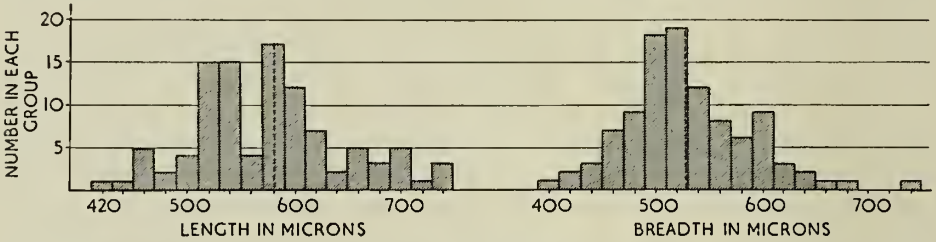
Only limited comparison is possible between the relatively well-preserved internal structures of *T. podolicus* and those of other species. It is not known whether the expansion of the middle part of the apical opening is a feature of other non-coronulate species, but coronulate species have a funnel-shaped opening (Peck, 1934: pl. 11, fig. 19). Although direct evidence of the cellular nature of the lime-shell is lacking in *T. podolicus*, the spiral ridges are presumably intercellular, as in the Russian species of *Trochiliscus*. The absence of furrows on the inner surface of the lime-shell, of regular radial interruptions in the concentric layering, and of ridges on the oospore membrane, may all be explained by non-induration of the radial walls of the spiral cells. A similar continuity of the lime-shell is presumably found in those Recent fruits which have oospore membranes with only faintly marked spiral ridges.

The layering of the lime-shell has not been clearly demonstrated in other species of *Trochiliscus*, few of which have been sectioned. Peck's sections of coronulate gyrogonites show a strongly concave, sometimes U-shaped or V-shaped, dark band in each transversely-cut spiral cell. These bands, which are apparently without stratification, much resemble those found in *Clavator* and *Perimneste* (Harris, 1939: 64, pl. ix, fig. 3). It may perhaps be doubted whether the bands represent the structure or layering in its original form, for the original lime-shell in all these specimens has been replaced by silica. There is, on the other hand, very close agreement between *T. podolicus* and *Sycidium* in the layering of the lime-shell, as Karpinsky's (1906: 105) detailed description and clear figures show. The only notable differences are that in *Sycidium* the banding is often regularly concave and thereby reveals the original cellular structure; and that the spacing of the bands is more than twice as great: Karpinsky gives an average of 11 $\mu$, which compares with 3–5 $\mu$ in *T. podolicus*. This difference in spacing is matched by the greater size and thickness of the *Sycidium* shells which have been figured.

Remains of the contents of the oospore have not previously been described, but the oospore membrane has been recorded from Europe and America. Karpinsky (1906: 157, text-fig. 58), in sections of trochilisks identified as *Sycidium*?, found that there were 'unverkennbare Spuren ihnen anhaftender vegetabilischer Membran' lining the inner surface of the lime-shell. He considered that this was very like the corresponding membrane in the Characeae. Peck (1934: 91, 98) recognized the oospore membrane in coronulate and non-coronulate specimens of *Trochiliscus* and also in *Sycidium*. His specimens are silicified and the membrane is preserved as a thin layer, or 'inner sphere of white cryptocrystalline silica', which is often contracted and folded, but is sometimes in contact with the lime-shell. A few of his sections, e.g. pl. 11, fig. 23, suggest that the original organic substance has not been completely replaced. For both *Trochiliscus* and *Sycidium* he described the membrane as an 'inner sac . . . suspended from the summit opening' (Peck, 1934: 95, pl. 11, fig. 13; pl. 13, fig. 16). This rather unusual appearance may be due to the contraction of the closed membrane away from the sides and base of the lime-shell, and its extension by displacement into the apical opening (cf. Text-fig. 2H).

## V. CHAROPHYTE AFFINITIES

It is unnecessary to restate the morphological considerations which led Karpinsky, and later Peck, to postulate the affinity of *Trochiliscus* with the Charophyta. Perhaps the most convincing evidence was Peck's demonstration that several North American species of *Trochiliscus* had apical structures, corresponding in number and position with the spiral cells, which could readily be interpreted as the cells of a calcified coronula. The present study of a new species of *Trochiliscus* has provided increased knowledge of the structure of the fruits, and the following detailed comparison with Recent and fossil charophytes confirms and strengthens this affinity.



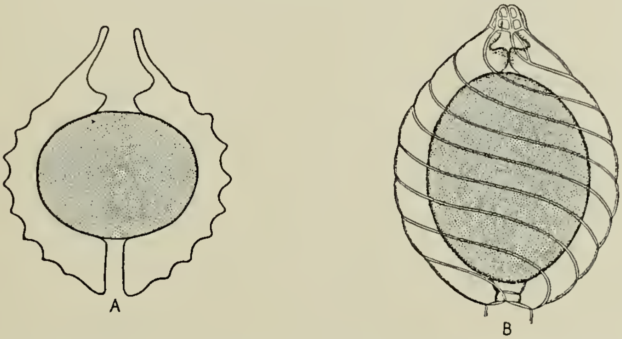
TEXT-FIG. 4. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. Histograms showing the size frequencies of 100 gyrogonites.

*Size variation.* There is an interesting and surprisingly close agreement between the size variations of the gyrogonite of *T. podolicus* and the equivalent measurements for the Recent *Chara vulgaris* and the Purbeck charophytes. Harris found that over 99 per cent. of a batch of 500 spores (oospores) of *Chara vulgaris* had lengths between the limits 610 $\mu \pm 20$ per cent. He found the same variation in the spore diameters, nearly all of which lay within ±20 per cent. of a mean. Similar results were given by Purbeck charophytes. The corresponding figures for *T. podolicus* are 97 per cent. (breadth) and 90 per cent. (length). The loss of the beak in many specimens is no doubt responsible for the greater variation in length, while the breadth measurements are affected, though to a lesser extent, by distortion of the specimens through compression. The variations are represented graphically in Text-fig. 4, which may be compared with Harris's text-fig. 16.

*Lime-shell.* The importance of the charophyte lime-shell needs no emphasis; yet no systematic study of its structure has been made. It is generally the only part of the plant preserved as a fossil, which is no doubt due to the special manner of its formation. In the calcareous Algae generally, and on the vegetative parts of many charophytes, lime is deposited as minute crystals in the mucilage surrounding the cell-walls (Fritsch, 1950: 62). The gyrogonite is exceptional in that the lime composing it is laid down in the interior of the enveloping cells and may largely replace their protoplasmic contents. An appreciable amount of calcium succinate, a soluble salt of calcium, is present in the cell-sap of *Chara* (Davis, 1901: 504).

The small basal opening in the gyrogonite of *T. podolicus* agrees generally with the equivalent opening in Recent and fossil charophytes. The lime-shells of recent

Chareae lack an apical opening, but it is present in some fossil species, and in the Purbeck Charophyta. As Karpinsky (1906: 130, 151) has pointed out, there is an opening between the distal ends of the uncalcified enveloping cells in young stages of *Nitella*. At maturity, if the coronula is dehiscent, antherozoids can pass directly into this opening, which is termed the 'neck-canal' by Migula (1897: 46). If the coronula is persistent, antherozoids enter the 'neck-canal' through slits between the enveloping cells. The 'neck-canal' may either be expanded distally, as in *Chara vulgaris*; or medially, as in *Nitella tenuissima*, when it much resembles the apical opening in *T. podolicus* (Text-fig. 5). See also Groves & Bullock-Webster, 1920: fig. 22, ii. The expanded portion is termed the *Scheitelraum* by de Bary (1871).



TEXT-FIG. 5. A. *Trochiliscus* (*Eutrochiliscus*) *podolicus* n.sp. L. Devonian. Gyrogonite in median longitudinal section. ×*c*. 55. B. *Nitella tenuissima*. Recent. Mature fruit. ×*c*. 90. After de Bary (1871).

The similarity of the layering of the lime-shell of *Sycidium* and *Chara* has already been noted by Karpinsky (1906). His pl. 3, fig. 14 shows a section of the lime-shell of a Miocene '*Chara*' cut parallel to the ridges, and he observes that the spacing of the light and dark bands is about the same as that of the finest layers in the shell of large species of *Sycidium*. A few of the gyrogonites of *C. hispida* sectioned for this paper show a faint but definite banding in places, the bands being about 4 $\mu$ apart, as in *T. podolicus*. Layering is much better shown by a gyrogonite of the fossil *C. escheri* (Pl. 19, fig. 28), although little or no indication of layering is given by the other 50 specimens on the same slide. The dark, more or less concentric, lamellae have an average spacing of about 3 $\mu$. The uniformity in the character and spacing of the layering in these lime-shells, allowing for the greater size of *Sycidium*, strongly suggests that the banding is an original feature of the lime-shell.

Karpinsky (1906: 129) ascribed the growth of the lime-shell to the layering of calcium carbonate particles within a mucilaginous or gelatinous substance. Layered concretions have been produced artificially by several workers by the precipitation of salts in the presence of organic colloids (Carpenter, 1901: 1100). Through the work of Schade much light has been thrown on the principles involved and on the relations between the visible structure of concretions, their composition, and the conditions under which they are formed. The lime-shell appears to be a good example of what Schade has termed *concrement formation*. He postulates that concrements, such as gallstones and ooliths, are built up in layers by the apposition of colloid and crystalloid particles. 'Precipitating colloids . . . produce a concentric layered structure, while crystalloids favour a radial striation. Where large percentages of both constituents appear, both types of structure coexist, interwoven' (Schade, 1928: 823). Ooliths, like the great majority of concrements, are composed of both crystalloids and colloids. When an oolith is treated with acid, the calcium carbonate (crystalloid) is dissolved and a distinct skeleton of silicic acid (colloid) remains. The lime-shell behaves in the same way. It has long been known that on removal of the lime the shell is represented by a delicate and closely stratified membrane (de Bary, 1875: 301). Migula (1897: 49) observed in thin sections of the shell that the delicate lamellae separating the calcareous layers were not destroyed by the acid, and concluded that they were possibly gelatinous. And Nordstedt (1889: 3) found that silicic acid was present in the oospore membrane. This substance may therefore be a constituent of the colloidal element in the lime-shell, as in ooliths and other calcareous concrements.

The close comparison between the structure of the layered lime-shell of the trochilisks and that of gallstones and ooliths showing secondary crystalline formation may be seen by examination of Schade's figs. 35, 36, 54, and 55. These figures show in places a very similar radial obliteration of the layering, due to transformation of the calcite, i.e. the growth of some crystalloid particles by the absorption of others. They also show indications of a radial striation; the breaking up of the dark bands into discrete, opaque, angular particles; and a slight and irregular undulation of the bands. Karpinsky (1906: 105, 151 et seq.) had already reached the conclusion that the radial striation of the lime-shell was due to recrystallization. On p. 105 he accurately described the dark bands in *Sycidium* as made up of minute, opaque particles, which he regarded as organic.

The small irregularities in the layering of the lime-shell, and the fact that the spacing of the bands does not gradually increase outwards, seem to exclude rhythmic precipitation after the type of Liesegang's rings (cf. Schade, 1928: 843).

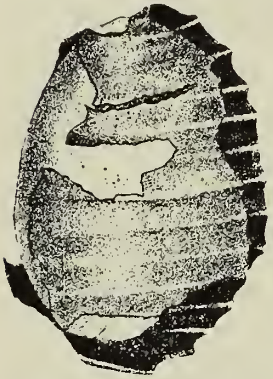
Although the banding of the lime-shell is seldom conspicuous in Recent or fossil gyrogonites, it is a significant structural character, especially well seen in the trochilisks. Similarity of structure betokens similarity of origin, and in this character also the trochilisks exhibit detailed agreement with the charophytes.

The lack of correspondence between the concentric layering and the ribbing or sculpture of the lime-shell in *T. podolicus* is still more marked in coronulate species of *Trochiliscus* if a U-shaped layering of their spiral cells be accepted. These examples seem to illustrate the commonly occurring 'independence of outer form and inner structure in an organic skeleton' (Sollas, 1921: 208). It has been shown that the tubercles of *Kosmogyra* are an integral part of the lime-shell (Reid & Groves, 1921: 185), and, according to Pia (1927: 90), they were developed late, the lime spirals being smooth at an earlier stage. In *Chara* (Karpinsky, 1906: fig. 40, p. 54; Reid & Groves, 1921: 182) and in *Sycidium* (Karpinsky, 1906: fig. 16) it is known that the final deposit of lime may considerably alter the appearance of the gyrogonite, and the various stages have been observed on the same specimen. The spirals, at first concave, may become flat, and finally convex; or, to use Peck's useful terminology, the first formed ridges are sharp and intercellular, later becoming rounded and cellular. According to Karpinsky (1906: 130, text-fig. 35, p. 50), the shape of the outer wall may be an important factor in determining the final form. Because of the variability of the sculpture within some species and even on the same specimen, this character has only a limited use in classification (for example, see Peck & Reker, 1948, on tubercles). In *Trochiliscus* a few of the coronulate forms figured by Peck have bipartite, or tripartite, ridges, which may be cellular or intercellular. In an important intermediate form, which is unfortunately not illustrated by a section, he found that two equal ridges represent each spiral cell, so that the number of ridges is twice the number of spiral cells. In *T. laticostatus* (Peck, 1934: pl. 11) the sculpture is exceptionally variable and it is difficult to feel convinced that all the forms are specifically related and differ from each other solely in the degree of calcification, especially as transitional stages do not seem to be developed on the same specimen.

*Oospore membrane.* The layered membrane forming the oospore wall has been studied in considerable detail in Recent charophytes, since its decoration, colour, and texture are characters of specific value (Allen, 1937). The tough outer layers, called the inner and outer coloured membranes by Groves & Bullock-Webster (1920: 56), are indurated and contain suberin (Nordstedt, 1889: 3; Overton, 1890: 36). The innermost layers directly investing the ovum are colourless and comparatively thin. The coloured and colourless layers are clearly shown by the Recent oospore in Text-fig. 6. In all species the outer coloured membrane is more or less strongly marked by spiral ridges or flanges derived from the lateral walls of the enveloping cells. In the Chareae the membrane is decorated with granules or tubercles. In the Nitelleae there are, in addition, reticulate types of decoration. The inner coloured membrane of all species is thinner and paler than the outer, and spiral ridges are not always shown; its decoration is always granulate, the granules being faintly, usually very faintly, indicated. The inner and outer membranes are often so closely adherent that they require a strong reagent to separate them (Groves & Bullock-Webster, 1920: 60).

There have been several records of the preservation of the oospore membrane in fossil charophytes. Reid & Groves (1921), for example, refer to well-preserved oospores in three species of *Gyrogonites* ('*Chara*') from the Eocene of Hampshire. But in no case has the decoration of the membrane been described and figured. Karpinsky (1906: 130) refers to the preservation of the membrane in *Lagynophora foliosa*. The photograph of *Lagynophora* sp. reproduced in Pl. 19, fig. 29, shows two fruits in approximately longitudinal section. The spiral ridges on the oospore membrane of the fruit on the left are cut tangentially. The oospore on the right, enlarged in Pl. 19, fig. 30, shows the somewhat contracted membrane in optical section; the transversely cut, broad-based ridges are clearly marked. This figure also provides definite evidence of a thin inner membrane. The figures of *Chara escheri* given in Pl. 19 show the excellent preservation of the original membranes in this Oligo-Miocene fossil; the detailed agreement with living *Chara* is pointed out below (p. 213).

The close comparison between the largely unaltered oospore membrane of *T. podolicus* and the membranes of Recent and fossil *Chara* is evident. Thus there is agreement in the brown, translucent character, and in the presence of a very similar granulate decoration. There is also some evidence of an inner and an outer layer. The way in which the fossil membrane has been cracked and disrupted in *T. podolicus* is closely paralleled in *Chara escheri*. The thickening of the edges of the minute pores through a few membranes of *T. podolicus* suggests a wound reaction. The only respect in which the oospore membrane of *T. podolicus* differs from those of Recent and fossil charophytes is in the absence of spiral ridges. Even in some Recent species, however, the ridges may be reduced to little more than faint lines (Groves & Bullock-Webster, 1920: 58).



TEXT-FIG. 6. *Chara fragilis*. Recent. Oospore with inner and outer coloured membranes partly scraped away exposing the intact colourless membranes. × *c*. 100. After Overton (1890). *Note*: The direction of the spiral ridges is reversed owing to the method of reproduction in the original.

*Oospore contents*. What is probably the true explanation of the origin of the vesicular contents of the oospore was suggested to me by Prof. T. M. Harris: that the vesicles represent starch-grains, the walls of the vesicles being the remains of the protoplasm and oil in which the starch-grains were embedded. The oospores of present-day charophytes contain oil and are tightly packed with rounded starch-grains. Some of these, showing the characteristic dark cross in polarized light, are represented in Text-fig. 1. Mirande (1919) stained the protoplasmic film surrounding the starch-grains with haematoxylin and found that 'les manteaux mitochondriaux, en contact serré, forment un pseudo-tissu cellulaire avec méats, d'où l'on peut, par une légère pression, faire sortir les grains d'amidon de leurs alvéoles'. His fig. 4 shows 'un fragment de ce pseudo-parenchyme mitochondrial dans lequel quelques grains d'amidon, contractés par déshydratation par l'alcool, se sont décollés des parois'. The same kind of structure is well illustrated in a section of the endosperm of maize (Sachs, 1882; fig. 50A), which shows polyhedral starch-grains surrounded by 'thin plates of dried-up fine-grained protoplasm'. The larger starch-grains of *C. hispida*, with a length of about 60 $\mu$, are of the same order of size as the vesicles of *T. podolicus* (cf. Text-fig. 1). These observations support the explanation given above. Similarly vacuolated cell-contents found in fossil pteridophytes and cycadophytes have also been attributed to starch-grains (Seward, 1898: 212, fig. 41 A, B).

There appear to be no records of the remains of the contents of the oospore in other fossil Charophyta.

Summarizing these comparisons between *T. podolicus* and Recent and fossil charophytes, we find very close agreement in the size variation of the gyrogonite, and in the structure of the lime-shell and of the oospore membrane; there is probably agreement also in the nature of the oospore contents.

The general morphological resemblance between *T. podolicus* and living *Chara* is brought out in Text-fig. 1. In some respects the comparison, especially of the apical region, is closer with *Nitella* (see Text-fig. 5), though the fruits of this genus are not calcified.

In spite of the demonstration by Peck of the presence of coronulate cells in *Trochiliscus* spp., reservations have continued to be held about the charophyte nature of the trochilisks, especially *Sycidium* (Pia, 1937: 776). But in view of the additional structural evidence given above, and taking into consideration the evidence that the trochilisks were probably non-marine plants (p. 209), the charophyte affinity of *Trochiliscus* now seems to be established beyond all reasonable doubt. No attempt has been made by authors to answer the very convincing case put forward by Karpinsky that *Sycidium* should be regarded as a charophyte. The ill-founded comparison between *Sycidium* and marine codiaceous Algae, especially *Ovulites*, is not supported by the occurrence of *Sycidium*, along with *Trochiliscus*, in non-marine deposits.

## VI. CLASSIFICATION OF *TROCHILISCUS*

Referring to Recent material, Groves & Bullock-Webster (1920: 86) have written: 'The Charophyta are extremely plastic, most species being subject to much variation of form . . .'; and on p. 88, 'aberrations from what is apparently the normal form of an organ in a particular species are common'. The charophyte gyrogonite has only a limited number of external characters by which species may be distinguished, and Groves (1933: 4) has referred to the hopeless task of trying to identify living species from 'imperfect detached fruits alone'. Harris (1939: 75 et seq.) has made a valuable survey of 'the relative magnitudes of the variation ranges of the individual species and of the family' (not including the trochilisks). He comes to the important conclusions that 'the range of the family does not appear great enough to allow a very large number of specific groups to be distinguished with any certainty'; and that 'the Charophyte gyrogonites are likely to be very difficult to determine specifically unless exceptionally abundant material is available, and even then difficult'. The inclusion of the trochilisks very considerably widens the range of form of the gyrogonite. In *Trochiliscus* the presence or absence of coronula cells, differences in the sculpturing, and in the number of spiral cells are additional characters for distinguishing species. Other characters may become available when the structure of more forms has been worked out.

When discussing the classification of the trochilisks Karpinsky (1906: 120) observed that the characters available for distinguishing species are generally variable and any classification based on them can claim to have no more than a provisional value. One of the characters to which he refers is the number of enveloping cells or ridges. Thus he included in *T. bulbiformis* forms with 8 or 10 as well as 9 ridges, and stated that *T. ingricus* 'usually' had 18 ridges. Similarly he recognized variation in the number of enveloping cells of *Sycidium* (p. 121). Peck (1934), on the other hand, while admitting some variation in *Sycidium* (p. 95), states his opinion that the number of spiral cells in *Trochiliscus* 'is a distinct morphological character . . . and a specific character of primary rank' (p. 102). Although the systematic value of this character has been considered at length by Karpinsky, it is necessary to return to the subject here because half the species of *Trochiliscus* recognized in America are distinguished by the number of enveloping cells alone and the same character is emphasized in a later paper dealing with structural trends in the Trochiliscaceae (Peck, 1936). The following observations provide further evidence in support of Karpinsky's view.

1. In each of three assemblages from different localities and horizons, Peck (1934: 103; 1936) found that the only constant difference between his species was the number of spiral cells or ridges. In the assemblage from the Mineola shale, which contained only non-coronulate forms, those with 10 ridges were common, while 9- and 11-ridged forms were comparatively rare, suggesting that the latter were variants of a 10-ridged species. Each of the other assemblages, those from the 'Sylamore' sandstone and the *Devonocidaris jacksoni* zonule, contained coronulate forms, which he divided into four species based on 8- and 9-celled specimens, which were abundant, and 7- and 10-celled specimens which were comparatively rare. In these two assemblages also it might be supposed that the rarer forms were variants of the commoner forms.

Peck (1934: 108) described *T. devonicus* (Wieland) from the Devonian of the Falls of Ohio as a non-coronulate form with 9 spiral ridges. '*Moellerina greenei*' Ulrich and '*Chara lemoni*' Knowlton also came from this locality, and they were stated in the original descriptions to have 'eight or nine strong angular, spiral ridges', and 'ten, or perhaps rarely nine, spirals (cells?)' respectively. The original figures and descriptions are more or less unsatisfactory, and the type material has not been traced. It is therefore of interest that five silicified specimens in the British Museum, labelled *Möllerina Greenei* Ulrich. Ohio Falls, U.S.A.,[1] should have 7, 8, 9, or 10 spiral ridges. The specimens agree generally in size, convolution, and shape with *T. devonicus*, and are alike except for the different numbers of spiral ridges. It appears therefore that the Falls of Ohio is a fourth locality in which this character shows an appreciable range.

2. Karpinsky (1906: 137) has emphasized the fact that the whorled parts of the plant which are homologous with the spiral cells are still very variable in Recent charophytes. Although the number of enveloping cells has been reduced to 5 in all genera since Palaeozoic times, naturally occurring variations in this number have been reported (Karpinsky, 1906: 136). Six spiral cells have been noted in a Recent and in a fossil fruit. Peck (1941: pl. 42, fig. 42) figures a 4-celled *Aclistochara* from the Cretaceous. In *Nitella*, 6, and in one case, 7, rudimentary enveloping cells have been seen in young 'oogonia'. Six, and 4, coronula cells have been found in *Chara*. Other teratological variations have been observed in abnormal fruits associated with normal reproductive organs. This abnormality takes the form of an additional whorl of enveloping cells, which show a tendency to twist in the same direction as the normal cells. The number of these enveloping cells is usually 5, but in *Chara foetida* there are sometimes only 4 (Goebel, 1918: 376), and in *C. contraria* var. *hispida* there may be 6 (Schmucker, 1927: 781). When both whorls are present, therefore, the total number of enveloping cells in Recent *Chara* may be 10 or, exceptionally, 9 or 11. It is very probable that such numerical variations, which are of no systematic value, were commoner in the earlier charophytes, as, for example, in *Sycidium*.

3. Numerical variation has of course been observed in many living plants, especially angiosperms, and the following example will serve to illustrate this. 'In the herb

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[1] These specimens were purchased at different times from Dr. F. Krantz, Bonn. Registered number V.13063.

Paris the flower is normally 4-merous, at least in *P. quadrifolia* and other species. But 5- and 6-merous flowers are exceedingly common as abnormalities, and this condition is the normal feature in *P. polyphylla*, in which even 7-merous flowers are not at all uncommon' (Worsdell, 1916: 60).

Very instructive parallels can also be found amongst fossil plants and animals. In the examples which follow there was not only considerable numerical variation (plasticity) in earlier species; but also, as in the Charophyta, a reduction in the number of parts in the course of geological time.

The first example is from the angiosperms. As a result of their study of the fruits of the London Clay and the Bembridge Beds, Reid & Chandler (1933: 42) found 'a considerable body of evidence pointing to reduction in the number of locules', and a greater variation in this number in earlier species. This is most clearly demonstrated by *Sparganium*. *S. multiloculare* from the Oligocene had 5-4-3-2-loculed forms; *S. ovale* from the Mio-Pliocene had 2- and 1-loculed forms; forms of *S. ramosum* from Interglacial beds had 4, 3, or 2 locules; and the living genus is usually 1-loculed, but two species are 2-loculed, and *S. ramosum* may rarely have two locules. 'The chain of evidence is rather interrupted and irregular, but undoubtedly points to a reduction in the number of locules having occurred.'

The other example is from the animal kingdom. With few exceptions the major part of the test in the Mesozoic and later echinoids is formed of 20 columns of calcite plates; but in the Palaeozoic echinoids the number of columns is variable and often great (Woods, 1947: 136). *Melonechinus multiporus* is an example of a Lower Carboniferous species in which the number of columns varies from 85 to 95 (Jackson, 1912: 375). Numerical deviation from regular penta-symmetry has been observed in many fossil and some Recent species of the Crinoidea (Bateson, 1894: 435). Bather (1889: 166) put forward the view that the Echinodermata were at first less definite in their plan of structure, but that through variation and natural selection the pentamerous type has become fixed. Much the same thing seems to have happened in the Charophyta.

4. Harris (1939) has shown that the size ranges of the Purbeck charophytes varied within a species by about ±20 per cent. of a mean. The gyrogonites of three species of *Clavator* were found to have a total range in length of 240–660 $\mu$. This may be compared with ranges of only 300–400 $\mu$, 700–1,000 $\mu$, and 600–800 $\mu$ given by Peck for the assemblages of *Trochiliscus* considered in the first section above. The range in each of these assemblages is less, not more, than the range in *T. podolicus*, which shows the normal variation. It must therefore be concluded either that size variation is of no value in delimiting closely allied species of *Trochiliscus*, or that fewer species are present than has been supposed.

For these reasons it is considered better not to regard the number of enveloping cells in each species of *Trochiliscus* as constant, but rather to recognize that there may be variations in this as in other characters of the gyrogonite. Although the number of spiral cells appears to be fixed in some species, in others there is evidence of a rather wide variation, e.g. from 7 to 10, or 9 to 11. The taxonomic changes required if such variation within a species be accepted are summarized below (p. 209).

The difficult question of the classificatory value of the sculpturing of the gyrogonite is touched on above, p. 202.

Regarding another character of the *Trochiliscus* gyrogonite, Peck (1934: 103) writes: 'Although the calcification of the coronula cells may be considered of greater than specific value, I have regarded it as a further trend towards calcification that might well be developed independently among species of different genera.' The calcification of the coronula cells is found in no other charophyte genus, *Aclistochara* excepted. It is therefore highly distinctive of those species of *Trochiliscus* in which it occurs. It is natural to assume that the apparently non-coronulate species of *Trochiliscus* had coronula cells which have not been preserved. If they were truly non-coronulate, the division between the coronulate and the non-coronulate species-groups would undoubtedly merit the establishment of a new genus for the former. But there does in any case seem to be a rather clear distinction between them: for the coronulate species have a large-celled coronula and a funnel-shaped opening; whereas the remaining species, when complete, usually have a beak with a small apical opening, which presumably supported a small coronula.[1] Peck (1934: 92) states that there is 'little possibility for mistaking these "non-coronulate" forms for "coronulate" specimens that have lost the coronula cells'. The distinction may be likened to that found in Recent charophytes: the coronula is well developed and persistent in *Chara*, and is inconspicuous and often deciduous in *Nitella* (Groves & Bullock-Webster, (1920: 53)). A further distinction between the two groups is that the spiral ridges of non-coronulate forms are simple and sharp and do not show the varied sculpturing of the coronulate species. The coronulate forms also show less range in size than the non-coronulate and are generally larger. It may also be significant that the known time ranges of the two groups are somewhat different: the non-coronulate forms are found in rocks of early Lower Devonian to Upper Devonian age; the coronulate forms in rocks of late Lower Devonian to basal Mississippian age. To give taxonomic expression to these differences it is proposed to group the coronulate forms in a new sub-genus which may appropriately be named *Karpinskya*, after the author who laid the foundation for all subsequent work on the trochilisks. The remaining, non-coronulate, forms are grouped under the sub-generic name *Eutrochiliscus*.

## *CHAROPHYTA*

### Family TROCHILISCACEAE

### Genus ***TROCHILISCUS*** Karpinsky 1906

Gyrogonites spheroidal or bulbiform, about 300–1,000 $\mu$ in diameter. Lime-shell externally (and sometimes internally) sculptured with continuous ridges or furrows representing about 7–18 dextrally spiralled enveloping cells, which originate around a cylindrical basal opening and extend to the summit; layered structure probably

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[1] In diagnoses of three non-coronulate forms—*T. devonicus*, *T. bellatulus*, and *T. rugulatus*—it is stated that 'a low ridge connects the apical ends of the spirals' (Peck, 1934). It seems from a comparison with the Mineola shale specimens, and other species, that this description should be applied to the basal, not the apical, ends.

more or less concentric and evenly spaced. Apical opening expanded medially or funnel-shaped. Coronula cells, when preserved, equal the enveloping cells in number and form a ring round the apical opening. Oospore filled with starch-grains (?). Oospore membrane resistant, originally suberised (?), decorated, probably two-layered.

### Sub-genus EUTROCHILISCUS nov.

DIAGNOSIS. Species of *Trochiliscus*, generally of small size. Coronula cells not known, probably small. Spiral ridges probably intercellular and equalling the enveloping cells in number.

SPECIES. *T. ingricus* Karp., type species; *T. bulbiformis* Karp.; *T. devonicus* (Wieland) Peck (*T. rugulatus* Peck); *T. convolutus* Peck (*T. minutus* Peck, *T. multivolvis* Peck); *T. podolicus* Croft.

DOUBTFUL SPECIES. *T.* (*Moellerina*) *greenei* (Ulrich); *T. lemoni* (Knowlton); *T. bellatulus* Peck.

DISTRIBUTION. Eastern Europe: Lower Devonian (Downtonian) to Middle Devonian. North America: late Lower (?) Devonian to Upper Devonian.

### Sub-genus KARPINSKYA nov.

DIAGNOSIS. Species of *Trochiliscus*, of medium and large size. Coronula cells large, calcified. Spiral ridges often multiple and then 2–4 times as numerous as the enveloping cells.

SPECIES. *T. laticostatus* Peck (*T. septemcostatus* Peck, *T. octocostatus* Peck, *T. decacostatus* Peck), type species; *T. bilineatus* Peck (*T. meeki* Peck, *T. liratus* Peck, *T. raricostatus* Peck); *T. herbertae* Peck.

DISTRIBUTION. North America: late Lower Devonian to basal Mississippian.

## VII. HABITAT OF THE TROCHILISKS

Recent charophytes live mainly in fresh water, though some species prefer brackish conditions; none can tolerate a normal marine environment. In the past also, charophyte remains are found typically in deposits laid down in fresh water, for example, the Purbeck lake beds.

Karpinsky (1906: 140) showed that in Russia trochilisks were very seldom associated with marine organisms, and concluded that the sandy and muddy strata in which they normally occurred were littoral, shallow-water, deposits. He further pointed out that the associated marine fossils in the American occurrences were not deep-sea but off-shore forms.

On this subject Pia (1937: 777) has written: 'Alle Forscher scheinen bisher der Ansicht gewesen zu sein, daß die Trochilisken und Syzidien meerische Versteinerungen sind (vergl. bes. PECK, 1934, S. 93 und 102). Um so überraschender ist es, daß HECKER, der beste Kenner des russischen Devons, sie jetzt (1935 *b*, S. 57–58) unter den Formen der Binnenbecken anführt, die in brackischen bis süßen, vielleicht aber stellenweise auch in übersalzenen Wässern lebten.'

More recently, Hecker (1941: 77, 81) points out that fishes and trochilisks frequently occur together to the exclusion of all marine invertebrates. He considers that the Middle Devonian beds in which *Trochiliscus* and fishes occur were laid down in 'running water' (Pärnu beds), and in a 'dying bitter salt lagoon gradually filled with delta sands and barkhans' (Narova beds). Of the Upper Variegated Series (Upper Devonian) he writes (p. 81): 'The marls enclose a multitude of trochilisks and most probably represent lake deposits.' In Podolia, as in Russia, *Trochiliscus* is associated with fishes and ostracods, and definite marine fossils are lacking. The Czortkov series consists of passage beds in which some marine horizons occur. The overlying beds of the Podolian Old Red contrast markedly with the contemporaneous marine beds of the region, and were almost certainly continental (mainly fluviatile) in origin (see Zych, 1927: 48; Samsonowicz, 1950: 504).

In the light of this evidence that the European trochilisks were probably aquatic land-plants, it is interesting to reconsider the American occurrences. It is true that *Trochiliscus* occurs, sometimes abundantly, in purely marine limestones, for example the Jeffersonville and Columbus limestones, along with a large marine shelly fauna of littoral type. It is, however, significant, and requires further investigation, that the beds from which Peck obtained much of his material, i.e. the Bushberg sandstone, the Grassy Greek shale, and the shale below the Mineola limestone, are all basal deposits, less than 30 m. thick, laid down in advancing and transgressive seas (Branson, 1922; 1944). The Bell shale, which forms 'a pocket in the Dundee limestone' (Peck, 1934: 116), and the Cerro Gordo substage of the Hackberry stage (Fenton, 1919: 358), are further examples. In such conditions it is possible that the mantle of a flooded land area has contributed to the deposits, and very probable that some of the sediments were laid down in brackish estuaries or lagoons. Indeed, in the Bushberg sandstone, Bell shale, and Grassy Creek shale, a marine shelly fauna is sparse or absent. Grabau, quoted by Branson (1922: 8), writes that the Noel shales (which are very similar to, and probably the lateral equivalents of, the Grassy Creek shale) 'can only represent the reworked residual soil of an old peneplain surface which was slowly submerged beneath the advancing Mississippian sea'.

The mode of occurrence of *Sycidium* in the Devonian of south-western China (Lu, 1948) is also very instructive.[1] The beds assigned to the Lower, Middle, and Upper Devonian of P'oshi in eastern Yunnan have a total thickness of about 1,660 m. Except for a few hundred metres of unfossiliferous sandstones at the base, the formation consists of a series of limestones, most of which contain a shallow-water marine shelly fauna, together with sandstone and shale horizons in which poorly preserved remains of vascular land-plants occur. The plants have been described by Hsü (1947), who assigns them to *Protolepidodendron*, cf. *Drepanophycus*, and other Devonian genera (see also Halle, 1936). In the highest and lowest plant-bearing horizons, marine shells are associated with the plants. No marine fossils, with the possible exception of the ostracods, are found in the series of beds which includes the limestone containing the abundant material of *Sycidium* described. This limestone is immediately overlain by a thick sandstone horizon with land-plants, *Lingula*, and

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[1] I am much indebted to Dr. J. Hsü, Curator of the Birbal Sahni Institute of Palaebotany, for providing me with a copy of this paper.

fish-remains. It is underlain by limestones with abundant ostracods at the base. Below these occurs the main plant horizon, consisting of 70 m. of sandstone with layers of shale. *Sycidium* is also found at a second, higher, horizon where it is associated with abundant corals in a succession of marine limestones. Hence the Chinese *Sycidium*, which is identified with the largest and commonest Russian species, *S. melo* Sandb., occurs in both marine, and non-marine or brackish, deposits. At the upper horizon the fruits may have been washed into a marine environment. At the lower horizon they may, like the nearly associated vascular plants, have been derived from the land, or have grown in brackish lagoons from which a marine fauna was excluded.

In this, as in many similar discussions on the environment of fossil groups, due weight must be given to the fact that while land-living organisms are frequently washed into the sea, marine organisms very rarely get preserved in continental deposits. It is therefore easier to explain the occurrence of fresh- or brackish-water trochilisks, even in abundance, in marine limestones than it is to explain the occurrence of marine trochilisks in equal abundance in lake or river deposits. Meek (1873: 219) wrote long ago that if the minute bodies in the Columbus limestone of Ohio were the fruits of the freshwater genus *Chara*, 'they must have been carried into the sea by streams, and deposited where we now find them, along with numerous marine shells'. The suggestion that tangles of charophytes may have drifted out to sea has been made by Groves (1933: 6). Cf. Pia (1931: 17).

It may be concluded therefore that the evidence from the American and Chinese occurrences of *Trochiliscus* and *Sycidium* generally supports that from Europe. At most horizons and localities in Europe, Asia, and America it is probable that the trochilisks had a fresh- or brackish-water, rather than a marine, habitat. At other horizons it may be assumed that the fruits were transported from the land into a shallow water, marine environment.

The preservation of the fruits of *T. podolicus* also gives a clue to their habitat. The infiltrated calcite in which the oospore membrane and contents are preserved may have been formed in the same way as in some Recent *Chara* marls, that is, by the redeposition of calcium carbonate dissolved by water percolating through the marl (Davis, 1901: 496); for it is probable from the worn nature of some of the specimens, and from the absence of vegetative axes, that the gyrogonites were derived from a contemporaneous deposit.

Supplementing the geological evidence on the habitat of the trochilisks is the biological evidence furnished by the fossils themselves. Among the freshwater Green Algae the membrane secreted round the egg after fertilization usually undergoes considerable thickening and constitutes a resting-spore in which abundant food reserves are stored. Such spores, of which the charophyte oospore is an example, are able to withstand prolonged desiccation and may retain their vitality over long periods. In the vast majority of marine Algae, on the other hand, there is no resting period and the zygote grows at once into another organism (Fritsch, 1935: 49, 50). The possession of a resting-spore with a 'lignified' or 'cutinized' coat was regarded by Church (1919: 30–32) as the most obvious criterion of those plants which had become partially or wholly adapted to life on land. Hence the demonstration that

*Trochiliscus* had large spores with a resistant (? suberised) wall, further protected by a thick lime-shell, and the evidence of food reserves in the form of starch, strongly suggest, when taken together, that the fossils were resting-spores of a plant which had already become adapted in some degree to a non-marine habitat.

## VIII. THE MORPHOLOGY OF *CHARA ESCHERI* UNGER

(Pl. 19, figs. 21–27; Text-fig. 7 a, c)

The following account of the well-preserved gyrogonites of this Tertiary species is the first illustrated description of the detailed structure of the oospore membrane of any fossil charophyte, other than *T. podolicus*. It brings out the fundamental agreement between the fruits of fossil and living *Chara* and at the same time strengthens the relationship between this genus and the Devonian *Trochiliscus*.

A synonymy of *Chara escheri* is given by Groves (1933: 17). This species was first clearly described and figured by Heer (1855) from Swiss material of Oligocene-Miocene age. The clearest figures are given by Unger (1860: pl. iv, figs. 1–5). Gaudin (1856) gave a detailed, but unillustrated, account of the morphology and confirmed Heer's observation that the lime-shell, when broken away, revealed the coal-black organic membrane surrounding the spore. The latter was filled with white calcite replacing the ovum. The microscopical characters of the spore membrane were not described. The homology of the lime-shell and the oospore membrane with the corresponding parts in Recent *Chara* was clearly recognized.

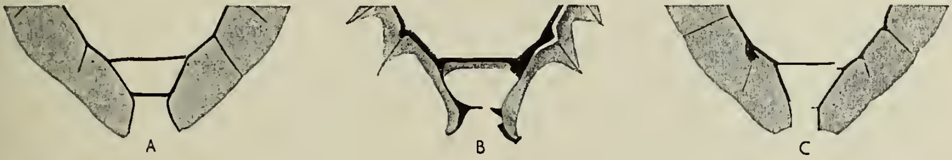
The material available for the present study is a piece of dark grey shale, registered number V.17236, containing numerous brown fruits which can be dug out with a needle. The specimen is labelled '*Chara Escheri* A. Br. Miocene. Rochette. Switzerland. Presented by Dr. Ph. De la Harpe.' It was in material from this locality that Heer (1855: 26) noted the presence of a black oospore membrane. According to Heim (1919: 130, 140) the Molasse at Rochette is of Upper Oligocene and Lower Miocene age.

The gyrogonites were treated in the manner described above for *Trochiliscus* (p. 192): about 50 were embedded together in one plane and sectioned; a small number were dissolved in hydrochloric and hydrofluoric acids, and the demineralized membranes were then mounted in gum chloral. Some of the gyrogonites are filled with pyrite in place of calcite, and patches of pyrite are often present in the somewhat recrystallized lime-shell. On decalcification the lime-shell maintains its shape and appearance. Between the lime-shell and the oospore membrane there is sometimes a thin layer of secondary silica.

Longitudinal sections (Pl. 19, figs. 21–23) show the structure clearly. The oospore membrane is plainly recognizable within the robust lime-shell; and the thickened lateral walls of the enveloping cells, which stand out as wide spiral flanges when the gyrogonites are demineralized, are well developed. At the base of the oospore the walls of the turning cell and the node-cell are thickened to form a well-marked cage, preserved in the same way as the oospore membrane. In one or two specimens there is a transverse partition across the cage (Pl. 19, fig. 23; text-fig. 7 a, c).

In only one of the sectioned specimens is the layering of the lime-shell clearly shown. The dark bands, which are rather evenly spaced at about 3 $\mu$, are more or less concentric with the oospore (Pl. 19, fig. 28).

The oospore membrane is double and about 5 $\mu$ thick. It is usually much cracked and disrupted. A few of the membranes from demineralized gyrogonites are perforated with irregularly spaced, rounded holes (Pl. 19, fig. 25) which have no doubt been bored by some organism. The outer membrane is dark brown and translucent with a semi-tuberculate decoration, the rounded granules being non-contiguous and of variable size (Pl. 19, fig. 24). The thin inner membrane is seen on torn edges and on the edges of the holes. It is pale brown by transmitted light and has a rather indefinite, granulate decoration (Pl. 19, fig. 26). The inner membrane is also seen in a few of the sections as a thin contracted brown line (Pl. 19, fig. 21). The spiral ridges on the membrane, marking the position of the lateral walls of the enveloping cells, are clearly shown (Pl. 19, fig. 24). The lateral walls, or flanges, are decorated with irregular granules which are coarser than those on the inner and outer membranes (Pl. 19, fig. 27). Remains of the organic contents of the oospore are not preserved.



TEXT-FIG. 7. The cage at the base of the oospore in longitudinal section. A, C. *Chara escheri*. Oligo-Miocene. V.28559. B. *Chara hispida*. Recent. V.28356. All × *c*. 75. (N.B. See Addendum, p. 216.)

It will be clear from a comparison with Text-fig. 1 B that there is a striking agreement between the structure of *C. escheri* and Recent *Chara*. The presence of a cage is especially interesting. The cages of the two species are compared in Text-fig. 7 (see also Text-fig. 1 B and Pl. 19, fig. 23). The statement by Groves & Bullock-Webster (1920: 58) that the cage at the base of the oospore encloses the stalk-cell appears to be inexact; for the 'transverse growth' to which they refer no doubt represents the thickened wall between the turning cell and the node-cell, or between the node-cell and the stalk-cell. Presumably it is the wall between the turning cell and node-cell, but there appears to be no statement on this in the literature (cf. de Bary, 1875: 300).

The layering of the lime-shell is discussed on p. 201 above.

The oospore membrane agrees in all respects with the equivalent membrane of existing charophytes. The inner and outer layers correspond to the inner and outer coloured membranes (Text-fig. 6) of Groves & Bullock-Webster (1920: 56). Pl. 19, fig. 24 of *C. escheri* may be compared with the decorated outer membrane of *C. vulgaris* in Pl. 19, fig. 20, and with the figures in Groves & Bullock-Webster. And the decorated inner membrane of *C. escheri* may be compared with the corresponding membrane of *Nitella* figured by the same authors (1920: pl. v, fig. 5). The decorated flange in Pl. 19, fig. 27 much resembles the flange of *Nitella* in their pl. iv, fig. 8.

The work on the Purbeck Charophyta has fully justified Pia's (1927) action in transferring *Chara*-like fossil fruits with five smooth lime spirals to a provisional genus, for which he has revived the name *Gyrogonites* Lamarck. This has been criticized by Peck (1941: 288) and by Rásky (1945: 29), who prefer to retain the name *Chara*. It is, however, clearly undesirable that a form-genus used for fossil material should bear the same name as a well-defined living genus; and there seems to be little risk of confusion between *Gyrogonites* as a generic name and 'gyrogonite' as a descriptive term, even when both words are capitalized. Harris (1939: 73, 74) finds that several of the fossil fruits formerly described as *Chara* cannot be distinguished with certainty from Purbeck species. It does not, however, seem possible to include *C. escheri* in *Perimneste horrida*, because the apex of the latter is uncalcified. Although it is not improbable that one or more extinct genera had an internal structure essentially like that of Recent *Chara*, the very close morphological agreement between the Tertiary form *C. escheri* and existing *Chara*, especially the presence of a cage at the base of the oospore, seems to justify the inclusion of this species in the living genus. According to Groves & Bullock-Webster (1920: 58) a cage is not developed in the Nitelleae. Wide spiral flanges are, however, more characteristic of *Nitella* than of *Chara*, but the fossil fruits are not laterally flattened as in that genus.

## IX. SUMMARY AND CONCLUSION

1. The genus *Trochiliscus* was founded on charophyte fruits (gyrogonites) from the Middle Devonian of north-west Russia and Esthonia—the only previous record from the Old World. It later proved to be well represented in Middle and Upper Devonian, and basal Mississippian beds in North America. The species described here, *T.* (*Eutrochiliscus*) *podolicus* n.sp., is from a new area, west Podolia, on the borders of Poland and Russia. It is of Lower Devonian (Downtonian) age and is the earliest charophyte of which there is reliable evidence.

2. The calcified gyrogonites are unusually well preserved and permit detailed comparisons to be made with living and extinct charophytes. General agreement is found with the fruits of *Chara hispida*, of which longitudinal sections have been prepared. In the shape of the apical opening of the lime-shell the comparison is closer with the uncalcified envelope of *Nitella* fruits. The layered structure of the lime-shell is very similar to that of living and fossil *Chara*, and also to that of *Sycidium*. The resistant, decorated, oospore membrane differs little from the corresponding membrane of living Charophyta and of the Tertiary species *Chara escheri*. A vesicular mass often present within the oospore membrane appears to represent the contracted starch-rich contents of the oospore. These new observations on the structure of the gyrogonites, and the demonstration that their size variations are almost the same as in *Chara vulgaris*, amply confirm the charophyte relationship of *Trochiliscus*.

3. The classification of *Trochiliscus* is discussed. Karpinsky's view that the number of spiral enveloping cells may vary within a species is upheld. Adoption of this view leads to a reduction of the number of species from about 17 to 8. The species are placed in two new sub-genera, *Eutrochiliscus* and *Karpinskya*, distinguished mainly by the presence or absence of large calcified coronula cells. The time range of *Eutrochiliscus* is from Lower Devonian (Downtonian) to Upper Devonian; and of *Karpinskya* from late Lower Devonian to basal Mississippian.

4. The trochilisks were considered by Karpinsky and by Peck to be marine plants. Recent stratigraphical work indicates, however, that the deposits in which the Russian trochilisks were entombed were continental, and hence that the plants probably lived in fresh or brackish water. The Podolian occurrence supports this view. Much of the North American material comes from basal deposits to which residual soils of invaded land-masses probably made a large contribution. In China, *Sycidium* occurs in abundance in a limestone between two sandstone horizons in which vascular land-plants, but no marine organisms, are found. The comparatively rare occurrences of trochilisks in littoral marine environments are probably to be explained by drifting. The resistant membrane round the oospore, which may have contained food reserves in the form of starch, indicates that the plants were adapted, like living freshwater Algae, to periods of desiccation. The conclusion is reached that the trochilisks were probably fresh- or brackish-water plants. This accords with the known habitats of living and fossil charophytes, and removes one of the reasons advanced against their Characeous affinity. In this connexion it is interesting to recall the contemporaneous occurrence of *Palaeonitella* in the Rhynie peat-bed.

The trochilisks seem to be rather typical of thin basal deposits laid down at breaks in the stratigraphical succession. For, in addition to several North American examples, the beds in the Leningrad area in which trochilisks are particularly abundant were laid down immediately above a major unconformity. In the absence of marine fossils, trochilisks are suggestive of fresh- or brackish-water conditions of deposition.

5. Important details of the structure of a Tertiary charophyte fruit, the Oligo-Miocene species *Chara escheri*, are described and figured for the first time; several points of agreement with *T. podolicus* are shown. The layered lime-shell, decorated oospore membranes, and cage at the base of the oospore agree closely with the corresponding structures in living *Chara* and justify the inclusion of the fossil species in the same genus.

6. We know through the work of Peck that there is a hiatus within the Carboniferous period between the ancient trochilisks on the one hand and the fruits of modern aspect with five spiral cells on the other; the two groups do not overlap in time, and, with the exception of *Palaeochara*, there are no intermediate forms. It is to be hoped that further collecting will bridge this gap. Despite these differences, the distinctive features of the fruits of both groups—the large oospore with a resistant membrane surrounded by enveloping cells in which lime is deposited to form a layered shell—have persisted essentially unchanged from a period not later than the early Devonian. The main trends have been towards a reduction in the number of enveloping cells, a loss of plasticity, and a change in the direction of coiling. In the early types the number of cells was less definite, often 8, 9, or 10, and up to 18, but the present number (5) had already become stabilized before the close of the Carboniferous period. By the same time, forms with straight enveloping cells (which were probably the most primitive), and dextrally coiled forms, had been completely replaced by forms with sinistral coiling. Comparable examples of reduction, with loss of plasticity, are noted in the fossil history of the echinoderms and of certain angiosperms. Judging from *T. podolicus*, the oospore membrane of *Trochiliscus* was very thin ($1\,\mu$), while

the equivalent figures for *Chara escheri* and *Chara hispida* are 5 μ and 10 μ, respectively. These figures appear to indicate a trend towards increased protection of the zygote against desiccation. The fact that the lime-shells of living charophytes are generally thinner than those of fossil forms may perhaps be correlated with it.

The Charophyta, which are related cytologically to the haplobiontic seaweeds, especially the Chlorophyceae, are of unusual interest in regard to the adaptation of marine Algae to subaerial conditions. Church (1919), in a detailed study of this question, referred to *Chara* as 'the transmigrant failure'. Bower (1935: 489) has attributed the 'stolid conservatism' of the charophytes to the fact that they did not 'hit on the innovation of postponing meiosis by interpolation of a diploid phase'. The trochilisks not only widen our conception of the Charophyta, and demonstrate that the fruits of the early charophytes were basically like those of today, but show that their earliest representatives were already adapted to a land habitat in very ancient times. The fact that the remains of trochilisks have not been found along with marine calcareous Algae in the extensively searched littoral deposits of Lower Palaeozoic age may be due to inadequate collecting. If this is not so, it suggests either that the development and calcification of their highly specialized fruits were delayed until they began to adopt a land habit; or that they had already emerged from the sea and become established on the land some time before the beginning of the Devonian period.

Pia (1940: 154; 1942: 12) has stressed the remarkable fact that the Devonian trochilisks came into prominence and reached their peak at a time when other calcareous Algae had greatly declined. Although it is difficult to account for the impoverishment of the marine calcareous floras, the local abundance of the Charophyta may be explained by evolutionary changes leading to the adoption of a new and more favourable environment in which there was probably little competition from other plants.

The much-debated affinity of the Charophyta is in no way elucidated by a study of their earliest representatives: they seem to have been just as isolated in the Devonian as they are today. The Charophyta stand out as a group that became highly specialized and adapted to life on land at a very early period, and has subsequently proved to be not only extremely conservative, but also remarkably persistent.

## ADDENDUM

The interesting account by Maslov (1947) of the structure of '*Chara*' *meriani* from Russian Tertiary deposits was not seen until this paper was in the press. The gyrogonites were studied in thin longitudinal sections, which demonstrated the two-layered character of the lime-shell, as well as other features. The inner layer has slightly concave or convex, concentric laminations, and it is clear from his drawings and descriptions that the banding of the calcite compares closely with that of other charophytes, for example, *C. escheri* (Pl. 19, fig. 28). The outer layer, however, which was evidently deposited on the outer wall of the spiral cells, is composed of clear, yellowish calcite, and does not show laminations. In a small number of specimens the inner and outer layers are separated by flattened tubular spaces representing the lumens of the spiral cells, and these spaces form a line of weakness along which the outer layer sometimes splits off. Deposition of lime in this way on both the inner and the outer walls of the spiral cells is not known in any Recent charophyte, nor in *C. escheri*, but it is a well-established feature of the Clavatoraceae (Harris, 1939: 36, text-fig. 71), and may have a wider significance.

Maslov also demonstrated that in his material the upper part of the basal opening of the gyrogonite is closed by a calcareous plate, a feature which had not previously been noted in the Charophyta. This basal plate, which is laid down on the inner wall of the turning cell, is also present in the living *Chara hispida* and is shown in Text-figs. 1 B and 7 B. A calcareous plate or plug of varied development also occurs in the basal opening of *C. escheri* and is erroneously omitted from Text-figs. 7 A, C. In this fossil species the upper surface of the plate, which is in contact with the base of the oospore membrane, is flat, or slightly concave or convex. The lower surface is usually more or less strongly concave and may be asymmetrical. In one or two specimens the plate is so thick that it fills the upper part of the basal opening, and in the specimen in Pl. 19, fig. 23 (but not shown in Text-fig. 7 A) its lower surface is in contact with the transverse septum.

It is clear that much has still to be learnt about the structure of the charophyte lime-shell, and it is very desirable that many more species, both fossil and Recent, should be examined in thin section.

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All the figures are from untouched photographs. The specimens in Figs. 1–5 were lightly coated with ammonium chloride. The photographs for Figs. 1–5, 15, 21–23, 29, and 30 were taken with Leitz Ultropak equipment. All the specimens figured, except Fig. 20, are in the Department of Geology, British Museum (Nat. Hist.). The transmitted light photographs were taken by Mr. H. M. Malies.

## PLATE 18

*Trochiliscus podolicus* n.sp., L. Devonian. Figs. 1–16. Pages 194–199.

Figs. 1, 2. Lateral and basal views of the holotype with 10 dextrally spiralled ridges springing from a small basal opening; 11–12 ridges are seen in lateral view. × 58. (V.28340.)

Figs. 3–5. Three gyrogonites in lateral view. The spiral ridges bend upwards on to the prominent beaks of two of the specimens. All × 58. (V.28338; V.28341; V.28339, respectively.)

Fig. 6. Median longitudinal section of a specimen freed from the rock. The basal and apical openings are clearly defined by dark infillings of matrix and reddish mineral. The central cavity of the lime-shell is filled with clear calcite. × 60. (V.28348.) Cf. Text-fig. 2e.

Fig. 7. Another specimen from the same slide showing the ridged lime-shell with apical and basal openings. The calcite of the central cavity extends into the narrow part of the apical opening, the expanded portion being filled with matrix. The contracted oospore membrane forms a ring enclosing traces of the organic remains of the ovum. × 60. (V.28348.) Cf. Text-fig. 2a.

Fig. 8. Equatorial section of a specimen in the rock showing the circular outline of the dark structureless lime-shell. The contracted oospore membrane is double as though an inner and an outer layer had separated. × 60. (V.28349.)

Fig. 9. Transverse section of specimen in the rock. The incomplete lime-shell shows regular layering throughout. × 60. (V.28352.)

Fig. 10. Part of Fig. 9 at a higher magnification showing the regular layering more clearly. × 180. (V.28352.)

Fig. 11. Another example of the regularly spaced, slightly undulating, layering of the lime-shell in a section of the rock. × 180. (V.28349.)

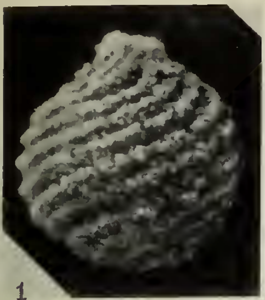
Fig. 12. Portion of the thick lime-shell of a specimen freed from the rock showing the ridges and rounded furrows in cross-section. The layering, faintly seen, appears to be more or less concentric and unrelated to the sculpturing. × 180. (V.28348.)

Fig. 13. Transverse section of a gyrogonite freed from the rock showing the ill-defined lime-shell, the disrupted oospore membrane, and the contracted vesicular contents with rounded outline. × 100. (V.28348.)

Fig. 14. Middle portion of a median longitudinal section through a gyrogonite. A few distinct rounded vesicles represent part of the oospore contents. A peak-shaped membrane attached to the oospore membrane projects towards the apical opening. × 180. (V.28348.)

Fig. 15. Globular vesicular body, still partly enclosed in the oospore membrane, dissolved out of a gyrogonite. × 94. (V.28347.)

Fig. 16. The contracted contents of a similarly treated specimen showing the vesicular structure clearly, at a higher magnification. × 180. (V.28346.)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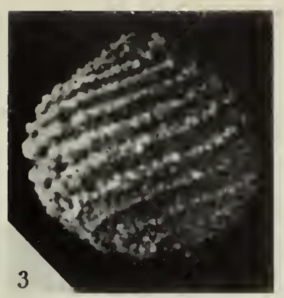
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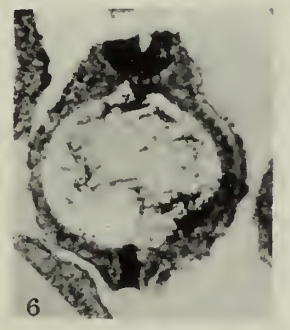
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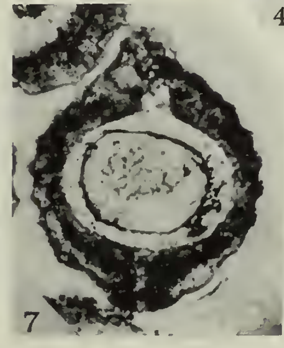
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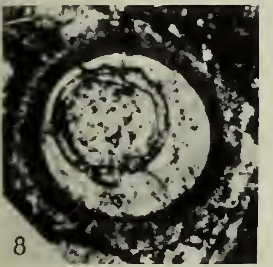
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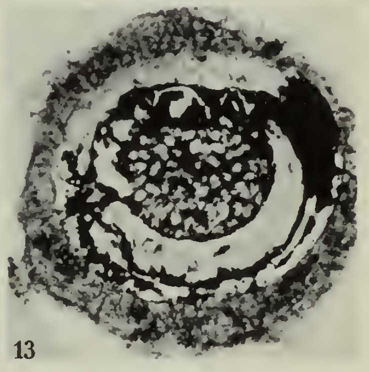
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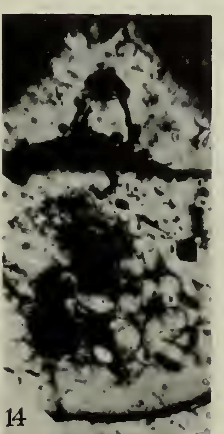
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*TROCHILISCUS*

## PLATE 19

*Trochiliscus podolicus* n.sp., L. Devonian. Figs. 17–19. Page 197.

Fig. 17. Portion of an oospore membrane, dissolved out of a gyrogonite, with a decoration of small irregular granules. × 500. (V.28346.)
Fig. 18. Portion of the oospore membrane of another specimen with a similar, but unusually coarse, decoration. × 500. (V.28345.)
Fig. 19. Oospore membrane, dissolved out of a gyrogonite, with more or less circular thickenings, some of which have a minute central pore. × 500. (V.28556.)

*Chara vulgaris* L. Recent. Fig. 20. Page 213.

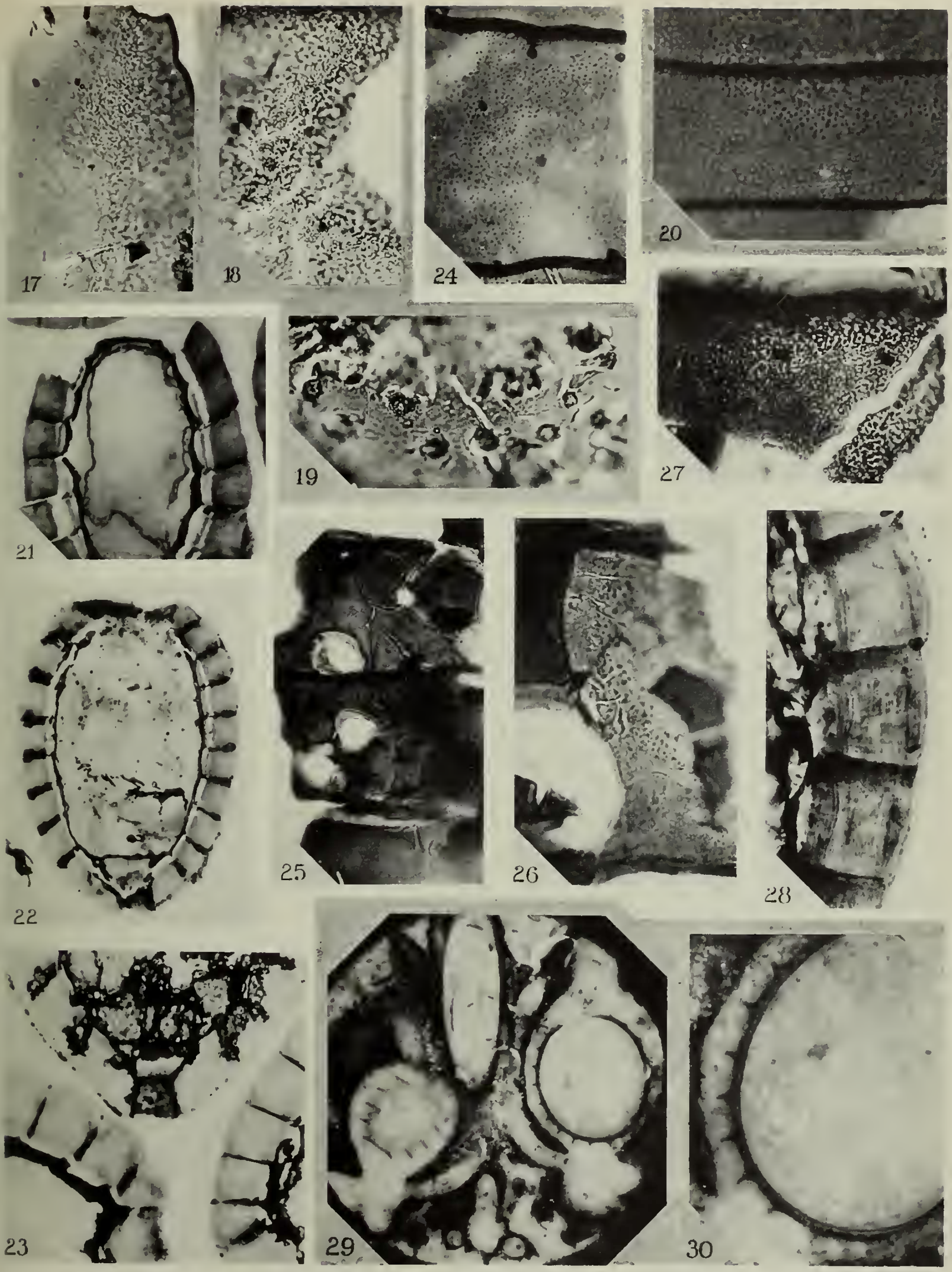
Fig. 20. Portion of an oospore membrane, for comparison with Figs. 17, 18, 24. The decoration is semi-reticulate, the rounded granules being non-contiguous and of variable size. The dark parallel lines are short lengths of the spiral ridges. × 500. (G. O. Allen Colln.)

*Chara escheri* Unger. Oligo-Miocene. Figs. 21–28. Page 212.

Fig. 21. The upper portion of a longitudinal section through a gyrogonite showing the outer oospore membrane and the thin inner membrane, which has contracted away from it. × 58. (V.28559.)
Fig. 22. Gyrogonite in longitudinal section. The thick lime-shell, basal opening, and black oospore membrane with prominent flanges between the lime spirals are clearly shown. × 58. (V.28559.)
Fig. 23. The lower portion of a gyrogonite in longitudinal section. The basal opening of the lime-shell is lined by a membrane forming a cage at the base of the oospore; the cage is divided by a transverse wall (cf. Text-fig. 7A). Portions of other gyrogonites show the well-developed flanges on the oospore membrane. × 86. (V.28559.)
Fig. 24. Oospore membrane with a semi-tuberculate decoration, the rounded granules being non-contiguous and of variable size. The spiral ridges to which the flanges are attached are strongly marked. × 485. (V.28560.)
Fig. 25. Portion of oospore membrane with three sub-circular borings. The inner, more translucent, membrane is seen on the edges of the holes. × 230. (V.28560.)
Fig. 26. Portion of a similarly bored membrane. The dark outer membrane has largely been removed exposing the thin inner membrane, which has a rather indefinite granulate decoration. × 485. (V.28560.)
Fig. 27. Portion of the spiral flange of an oospore with a well-marked decoration of irregular granules. × 485. (V.28560.)
Fig. 28. Portion of the wall of a gyrogonite in longitudinal section showing the fine banding of the thick lime-shell and the convex profile of the lime spirals. The black disrupted oospore membrane is seen on the left. × 175. (V.28559.)

*Lagynophora* sp. Eocene (Liburnian). Figs. 29, 30. Page 203.

Fig. 29. Approximately longitudinal section through a fertile node exposed on a polished surface of the rock. In the fruit on the left the spiral ridges of the oospore are cut tangentially; in the fruit on the right they are cut transversely. × 36. Monte Spaccato, Trieste. (V.17155.)
Fig. 30. Portion of the oospore on the right of Fig. 29, enlarged. The strong spiral ridges on the oospore membrane are seen in transverse section; in places the thin inner membrane has become separated from the outer membrane. × 94. (V.17155.)



TROCHILISCUS, LAGYNOPHORA, CHARA